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CLONAL VARIATION IN PECTINATELLA

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The freshwater Bryozoan *Pectinatella magnifica* produces, as is well known, lenticular statoblasts or winter buds that carry at the margin hooks whose number varies from 11 to 26. The statoblasts develop in the funiculus of the zooids. The zooids arise by budding from embryonic tissue which is laid down even in the statoblast-embryo of the preceding generation. The zooids of a colony are thus related as closely as possible, being developed parts of one and the same germplasm. The zooids of a colony are found in branches or twigs that radiate from a center and, in *Pectinatella,* are thick, short and blunt, forming a stellate colony. Many of these corms lie in contact with each other on the surface of a more or less spherical mass of jelly that is secreted by the colony. The colonies are in close contact like the facets of a compound eye. As the gelatinous mass increases so does the area available for the colony and thus additional space is allowed for their growth.

Whence come the colonies that lie on the surface of any one of the gelatinous masses? In part they arise by fission of preexisting colonies. A given colony gains an elliptical shape and then constricts in the short axis; the periphery of the colony is increased and room made for new branches and new young buds. If all colonies on the surface of a given mass arose thus we could refer the origin of them all to the original colony that came from the statoblast. But, unfortunately, things are not so simple. For two statoblasts may germinate in close proximity to each other on the same substratum and, under such circumstances, the masses of jelly they secrete will flow together and form parts of a single mass. Thus the gelatinous masses in nature are of two sorts:

simple, all of whose colonies (and included statoblasts) carry the same germplasm and *compound,* those whose colonies and statoblasts carry more than one kind of germplasm. These can not, in general, be distinguished by gross appearance.

Recent studies have shown that parts of organisms that are derived from the same germplasm (without the intervention of sexual reproduction) are much more constant in their morphological features than parts of organisms that, however closely related, are each the product of the union of two germ cells. For germ cells are necessarily more or less unlike, and may be very unlike, and, consequently, their progeny will be variable. We should expect then (to return to the *Pectinatella* masses) to find them of two kinds, (*a*) with a relative constancy in the modes of the distributions of the statoblast-hooks, and (*b*) with two or more modes (centers of variation) of statoblast-hooks in different colonies from the same mass.

HISTORICAL

The first statistical study of variation in the number of hooks per statoblast made was, in 1900, by one of us. In 1906, Miss Alice W. Wilcox showed that a *Pectinatella* mass is derived from statoblast-embryos the products of which repeatedly divide, move from each other and, as they enlarge, come in contact again. Her study makes it probable that a mass may be derived either from one or from two or more independent statoblast-colonies. Braem (1911, pp. 321, 323) refers to a mass derived from about 80 statoblasts, but the product of a great proportion of them perished. He has also a mass derived from only one statoblast. Braem points out that the number of hooks per statoblast tends to increase with the age of the colony and of the whole mass. He considers a possible difference in heredity tendencies inside the different colonies and concludes that this factor is small as compared with other factors, above all, temperature of the water.

Thus he finds that, in one and the same colony, the mean number of hooks increases with the temperature of the colony when the hooks are being formed and, in support of this contention, gives tables of his countings from the same mass between July and October. Some of his data support this conclusion strongly, as shown in Table I.

TABLE I

Braem's Serial Number.	Date of Examination.	No. of Statoblasts Counted.	Average Number of Hooks.	Description of Mass.
24	Aug. 23	30	14.33	Derived from 5 statoblasts. First statoblast June 28.
25	Sept. 14	12	17.50	From peripheral zone.
26	Sept. 14	34	18.47	An offshoot from the same mass.
18	Sept. 6	145	14.12	Derived from 2 statoblasts.
19	Sept. 24	441	14.69	Oldest portion.
20	Sept. 24	302	15.44	Peripheral (younger) zone.
21	Sept. 24	81	16.65	Youngest zone.
22	July 16	3	13.33	First statoblast.
23	Aug. 3	56	15.52	

In other cases the hypothesis is not sustained as shown in Table I*a*.

TABLE I*a*

Braem's Serial Number	Date of Exam.	No. of Statoblasts Counted	Average Number of Hooks	Description of Mass
10	Aug. 7	32	12.94	Mass from 1 statoblast, 1st statoblast.
11	Aug. 31	287	14.21	Same mass.
12	Sept. 10	235	13.82	Same mass.
13	Oct. 5	440	14.47	Same mass.
14	Aug. 31	258	14.56	
15	Sept. 15	365	14.30	

The remaining series have determinations at two dates only and are less significant, though supporting the hypothesis, so far as they go.

Influence of Age on the Number of Hooks

In our work, colonies of *Pectinatella* were grown on a clean board kept at the dam, lowest lake, Cold Spring Harbor, and examined daily. The first young colonies that attached themselves to the board in June were doubtless statoblast colonies (although the shell of the statoblast was not found) as no embryos were seen until July. None of the colonies formed statoblasts during June, but began to form them early in July. At various dates some of these elementary colonies were removed from the board and the hooks of their statoblasts counted. Later the separate colonies grew together and their origin became confused, but it is certain that the sets of statoblasts given in Table II are each derived from a single statoblast-ancestor. All statoblasts that possessed well-developed hooks were counted—there was no selection.

TABLE II

DISTRIBUTION OF FREQUENCIES OF NUMBERS OF HOOKS PER STATOBLAST IN EACH OF SEVERAL COLONIES, COUNTED AT DIFFERENT DATES

Date, 1912	Number of Hooks										Average
	12	13	14	15	16	17	18	19	20	21	
July 6			5	9	5	1					15.1
July 9			1	2	2	1					15.5
July 9			3	3	4	2	1			1	16.0
July 17[1]	1	1	3	6	7	6					15.5
July 17[2]			4	27	16	6					15.5
July 19		1	9	24	5	5					15.1
July 19	1	4	10	10	6	2					14.7
Aug. 8			2	14	9	3	1				15.5
Aug. 8[3]			3	4	1	1					15.0
	2	6	40	99	55	27	2	0	0	1	

Our studies, though not made on one and the same simple mass at successive periods, have been made on several colonies early in the season (beginning July) and at the end of the season (October). Counts on 241 statoblasts from 13 colonies made in July average 15.3 hooks; 7,255 statoblasts of one mass made in October gave an average of 15.6 hooks; 5,593 statoblasts from a probably complex mass counted at the same time in October gave an average of 16.0 hooks. Thus the difference between two sets of counts made in the same month on two distinct masses is greater than between the July and October counts. The highest average number of hooks found in any mass during October was in Mass *B,* 3,802 individuals, with an average of 16.6 hooks.

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[1] Many undeveloped.

[2] Few, if any, undeveloped. The two colonies taken on the 17th were small, adjacent and attached to each other. Probably from the same statoblast.

[3] Colony in full life and vigor; immature statoblasts on funiculi.

Comparing with Braem's, it appears that our counts run much the higher. The average of all counts made by Braem is 14.34, which is decidedly lower than our July average (15.3); and in one colony he obtained an average of 12.94 hooks. A great mass found at Jackson Park, Chicago, in August, 1898, gave an average of 13.78 hooks. It is clear, accordingly, that however important the temperature factor may be,[4] it is secondary in importance to some other factor that determines the variation in the number of hooks.

The number of hooks is determined by the number of pocket folds arising in the membrane that secretes the chitinous covering of the statoblast; and the question now transfers itself to the reason why in some statoblasts few, in others many, such folds occur. At one time we entertained the hypothesis that there was a causal relation between thickness of membrane and the size of and distance between pocket folds, such that a thin membrane permits smaller and more numerous folds. Unfortunately, it was not feasible to measure the thickness of the setigerous membrane, for by the time the number of eventual hooks can be determined the membrane has become relatively thin and very irregular in thickness. Our study did serve to indicate that the number of hooks can not be determined in a mechanical way by the thickness of the membrane, but that, on the contrary, the folds follow, and their number is determined by, the number of centers of cell keratinization. In some statoblasts the number of these centers is small; in others great.

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[4] Unfortunately, we made no thermometric determinations of the temperatures of the lake water. The lake is spring fed and shaded around the edges. As a guess, it rarely exceeds 20° C. in temperature; the July temperature is probably about 18°.

To test the hypothesis that the size of the cells in the setigerous membrane covering the statoblast influences the number of folds arising in it, we measured the diameter of the facets on the disc and on the float of statoblasts with 20 hooks and those with 12 hooks. The average diameter of a facet on the disc in 25 measurements (each based on a row of facets) was, in statoblasts with *20 hooks, 8.37 μ; in statoblasts with 12 hooks (14 sets of* measurements) 8.25 μ. On the float, in statoblasts with 20 hooks, 9.54 μ, in statoblasts with 12 hooks, 9.40 μ. It results first, that the facets (cells?) of the float are slightly larger than those of the disc, but that the difference in size of the facets in statoblasts with many and those with few hooks is neglible.

Since there seems to be nothing in the interrelation of parts to determine that the number of hooks shall be great or small one is naturally led to suspect that in these varying statoblasts we are actually dealing with distinct biotypes. We turn, consequently, to that phase of the question. The ideal conditions for an answer to the inquiry whether there are distinct biotypes in respect to number of hooks are these: To plant several statoblasts (with varying number of hooks) from each of the several independently arisen colonies and count the number of hooks on the statoblasts that are produced therefrom. We have not abandoned the hope of meeting these conditions, but our attempts to do so have hitherto been frustrated. Of nine statoblasts affixed (by shellac) to submerged wood none hatched. Also, colonies observed daily from hatching were eaten up by the larvæ of caddis flies (*Hydropsyche*). Finally after we had secured a good development of colonies free from predaceous insects all our work was brought to naught by the destruction of our floats.

We have, however, sought to get the required information in a more indirect way. We have studied the number of hooks on statoblasts from different masses in order to see if there was less variation inside of one mass than between different masses. This method has its clear limitations; for one does not know whether a given mass is simple or compound in origin. If, in any large mass, the modes, or the average, of the number of hooks varies greatly between colonies, that is evidence of the compound nature of the mass. If, on the contrary, the averages of all the different colonies of a mass are closely alike that indicates the homogeneity and probably simple nature of the mass—its origin from one statoblast.

TABLE III

MASS 1

Colony No.	*N*	11	12	13	14	15	16	17	18	19	20	21	Average
1	460		4	22	148	324	272	165	48	10	7		15.62 ± 1.26
2	884		2	37	145	303	259	173	46	26	8		15.66 ± 1.36
3	828		1	33	165	320	243	155	72	9	1	1	15.58 ± 1.30
7	720		6	31	136	324	283	132	76	7	4	1	15.62 ± 1.30
8	523		2	41	166	296	249	166	63	11	4	2	15.59 ± 1.33
10	361			31	155	335	241	161	69	8			15.59 ± 1.25
12	508		2	30	189	319	242	120	59	35	4		15.57 ± 1.39
13	337			39	134	305	258	130	92	39	3		15.75 ± 1.42
14	288			63	180	270	230	139	104	4			15.57 ± 1.43
17	326			28	150	337	240	153	77	15			15.63 ± 1.28
18	401		3	45	207	331	217	154	30	10	3		15.36 ± 1.26
20	348		3	26	155	313	273	152	69	9			15.60 ± 1.25
21	560			39	179	332	257	146	43	4			15.44 ± 1.19
22	439	2	2	18	158	291	265	164	87	11	2		15.70 ± 1.32
24	272			26	143	298	268	180	63	18	4		15.71 ± 1.30

TABLE IV

MASS 2

Colony No.	*N*	12	13	14	15	16	17	18	19	20	21	26	Average
1	689		20	130	251	282	190	101	23	3	1		15.91 ± 1.35
4	284		10	67	240	278	240	144	18	4			16.19 ± 1.27
6	679	2	25	113	260	299	205	83	10	3			15.88 ± 1.27
10	646		14	128	243	274	189	108	43				15.99 ± 1.37
16	501	6	12	106	281	291	192	84	26	2			15.89 ± 1.30
20	387		26	109	299	307	163	80	13	3			15.78 ± 1.25
24	277			83	220	310	238	116	25	7			16.18 ± 1.25
26	354		11	79	198	308	249	127	23	3		3	16.23 ± 1.36
30	367		16	93	237	308	250	85	11				15.98 ± 1.20
31	250		8	84	260	260	232	112	44				16.14 ± 1.31
33	240		8	75	283	237	230	154		13			16.13 ± 1.30
34	308		16	117	253	263	214	123	10	3			15.97 ± 1.31
35	205		15	98	230	351	205	63	34	5			15.99 ± 1.26
36	308		10	71	198	341	257	84	26	13			16.19 ± 1.25
40	259		12	16	286	305	220	93	15	4			16.02 ± 1.20

In any case the data collected have an interest of their own and are herewith put on record.

TABLE V

MASS 3

Colony No.	N	11	13	14	15	16	17	18	19	20	Average
1	646		15	70	271	280	210	121	28	5	16.10 ± 1.30
3	746	1	11	101	243	291	213	111	16	13	16.06 ± 1.33
4	708		20	105	196	253	237	151	30	8	16.20 ± 1.41
5	513	2	16	94	270	311	214	72	14	8	15.92 ± 1.24
8	362	5	22	77	254	293	207	105	25	11	16.04 ± 1.37
9	282		7	85	262	252	227	124	39	4	16.15 ± 1.33
15	442	5	32	152	290	265	167	66	18	5	15.66 ± 1.35
17	421	2	7	71	195	237	197	207	59	26	16.53 ± 1.51
18	297		10	125	266	226	215	128	30		16.02 ± 1.36
22	488		4	82	240	305	195	131	33	10	16.18 ± 1.33
24	271		11	92	214	262	196	148	63	15	16.31 ± 1.47
25	419	2	7	88	224	344	215	86	31	2	16.06 ± 1.24
26	279		7	50	172	211	283	168	79	29	16.68 ± 1.45
31	236		8	47	170	343	280	102	42	8	16.36 ± 1.23
32	221		5	68	172	240	231	190	77	18	16.59 ± 1.45

TABLE VI

MASS 4

Colony No.	N	12	13	14	15	16	17	18	19	20	21	Average
1	342		12	73	208	292	237	123	50	6		16.27 ± 1.34
2	278	4		25	97	255	238	212	94	50	25	17.11 ± 1.54
3	269		4	41	119	197	204	290	104	41		17.05 ± 1.47
5	356		6	45	180	213	225	188	82	56	6	16.81 ± 1.58
6	559	2	16	140	265	286	170	89	29	4		15.85 ± 1.35
7	537			30	132	276	238	212	73	30	9	16.86 ± 1.40
8	231			39	126	177	307	230	78	43		16.97 ± 1.40
10	268		4	26	134	231	250	220	93	34	8	16.44 ± 1.44
12	299	3	10	94	291	271	211	101	13	7		15.95 ± 1.27
13	158			25	171	241	234	228	82	13	6	16.80 ± 1.37
14	254			31	134	217	272	225	71	51		16.94 ± 1.41
15	253			24	174	245	170	253	87	39	8	16.91 ± 1.49
16	156			32	141	160	320	192	109	45		17.01 ± 1.43
17	198		5	40	136	227	237	177	116	51	10	16.96 ± 1.57
18	132			30	167	258	212	250	68	15		16.75 ± 1.34

Note.—Each of the Tables III–VIII, gives for a number of separate colonies of one and the same mass the frequency of occurrence of each number of hooks to a statoblast. The actual number of statoblasts counted is given in the column headed N; the columns to the right of N are for the entries corresponding to the number of hooks named at the top of the column; the frequencies are reduced to 1,000 statoblasts per colony. The column at the extreme right gives the average number of hooks for each colony together with the standard deviation of the distribution.

TABLE VII

MASS 5

Colony No.	*N*	12	13	14	15	16	17	18	19	20	21	22	Average
1	239			13	104	268	242	214	101	50	8		17.08 ± 1.41
2	572		5	24	113	217	217	230	144	45	5		17.14 ± 1.50
7	213				75	263	258	282	70	28	19	5	17.19 ± 1.33
8	179			22	112	223	330	196	61	45	11		16.98 ± 1.38
9	177			6	85	237	305	237	85	45			17.12 ± 1.26
11	107		9	56	141	150	234	196	159	56			17.05 ± 1.64
15	116			17	76	190	268	319	104	26			17.21 ± 1.26
16	78				103	244	308	218	90	24	13		17.08 ± 1.29
20	163		6	12	61	203	203	320	98	85	6	6	17.44 ± 1.48
21	337			15	83	160	297	210	142	74	18		17.42 ± 1.48
22	323		25	99	235	272	189	118	53	9			16.11 ± 1.46
24	336		3	77	223	283	202	122	63	24	3		16.36 ± 1.46
31	272		7	66	239	280	184	165	52	7			16.31 ± 1.38
32	357	6	53	216	289	240	126	62	8				15.38 ± 1.33
34	333	18	69	222	291	228	102	54	12	3			15.24 ± 1.41

TABLE VIII

MASS 6

Colony No.	*N*	12	13	14	15	16	17	18	19	20	21	22	23	24	26	Average
1	461		2	20	128	260	217	215	74	48	13	13	7	2	2	17.11 ± 1.72
2	617		20	110	306	298	183	70	10	2						15.77 ± 1.20
5	484		12	105	277	351	161	72	17	4						15.85 ± 1.21
6	531	2	19	158	335	258	149	60	19							15.61 ± 1.25
12	470		26	68	215	274	228	157	28	4						16.22 ± 1.36
14	492	8	37	173	260	211	185	96	26	4						15.72 ± 1.48
20	252		16	64	190	266	238	159	52	12	4					16.40 ± 1.42
25	45			44	67	178	222	378	89	22						17.18 ± 1.32
31	650	2	37	142	317	283	154	58	6	2						15.58 ± 1.24
47	171	6		76	111	251	263	175	99	18						16.70 ± 1.47
49	322		6	146	280	295	193	62	16	3						15.79 ± 1.23
50	278	14	58	212	330	205	126	51	4							15.25 ± 1.31
51	200				65	185	225	275	100	120	20	10				17.65 ± 1.53
52	280	4	25	125	310	250	186	89	7	4						15.75 ± 1.30
53	340		3	50	217	282	209	170	47	18	3					16.45 ± 1.38

From Tables III to VIII it appears that certain *Pectinatella* masses are characterized by a great constancy in the modal and the average number of hooks in a colony. Thus, in Table III the range in the average is only from 15.36 to 15.75, or 0.4, and the modal number of hooks is constantly 15 in all colonies of the mass. So, too, in Table IV with one exception the mode of the 15 colonies is 16 despite the fact that the average for the whole mass is near the dividing line between 15 and 16, viz., 16.03. The remaining masses show a greater or less commingling of biotypes. Thus, in Table V the empirical mode varies from 15 to 17 and the range of the average number of statoblast hooks to a colony is .76. In Table VI the mode ranges from 15 to 18 and the range of the average is 1.20. Tables VII and VIII show masses 5 and 6 to be even more variable with a range of 2.40 hooks in the averages.

Examining the standard deviations, we find no evidence that, except for the fact that, as is usually the case, the standard deviation tends to increase with the average, the great variability of masses 5 and 6 is due to a corresponding variability inside the individual colony.[5] We conclude, consequently, that the difference in variability between masses 1 and 2, on the one hand, and masses 3 to 6, on the other, is due to the fact that the former are simple in origin and the latter are compound; the former represents one biotype, the latter two or more biotypes. Compare the pairs of distributions in Table IX for mass 1 and mass 6—the most unalike having been selected in each case.

TABLE IX

COMPARISONS OF TWO UNLIKE DISTRIBUTIONS IN

MASS 1

No. of Hooks	12	13	14	15	16	17	18	19	20	21	22	Average
Colony 13		39	134	305	258	130	92	39	3			15.75 ± 1.42
Colony 21		39	179	332	257	146	43	4				15.44 ± 1.19
MASS 6												
Colony 50	14	58	212	330	205	126	51	4				15.25 ± 1.31
Colony 51				65	185	225	275	100	120	20	10	17.65 ± 1.53

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[5] The highly exceptional colony 1 of mass 6 being neglected. Unfortunately, we have no data concerning the position on the mass of this remarkable colony. In a paper just received from Braem (1913) a similarly highly variable colony is described.

The difference between the members of the first pair is chiefly in the scattering of the distribution—in the variability—inside the colony. The difference between the members of the second pair is a difference of mode—of type. These latter two distributions, and others in Table VIII, have little in common; they are the product of distinct biotypes.

Inside of a single biotype—inside of a single colony—there is a great variability in the number of hooks. Why is this? Unfortunately, we do not know. The query is one with others concerning the cause of variability, upon which we hope to shed some light.

Our study suggests that the difference in the average number of hooks in mid and late summer statoblasts is not due merely to the differences of age, temperature and food conditions in these two seasons, but probably also to the circumstance that the biotype that forms many hooks is one that develops later in the season than the others. Our study has, indeed, solved few problems, it has rather shown what a fine field for investigation is offered by the remarkable variation of the hooks on the statoblasts of *Pectinatella.*

COLD SPRING HARBOR, N. Y.,
February 25, 1913

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